Body Weight and Survival of *Calosoma sayi* (Coleoptera: Carabidae) During Laboratory Feeding Regimes

ORREY P. YOUNG[1]

USDA–ARS–SGIRL, P.O. Box 748, Tifton, GA 31793

ABSTRACT   Laboratory feeding trials were conducted with 40 adult *Calosoma sayi* DeJean (Coleoptera: Carabidae) over a 19-wk period, by using as food either the larval, prepupal, pupal, or adult stages of the fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae). The mean survival period of the beetles maintained on the separate fall armyworm stages was 122 d (larvae), 75 d (prepupae), 57 d (adults), 34 d (pupae), and 31 d (no food). All beetles offered food weighed less at death than at the beginning of the experiment, even though the percentage of gain in body weight during the experiment ranged from 25% (pupae) to 40% (prepupae). Those denied food gained no weight and lost >19% body weight before death. The only significant difference between the sexes was in the percentage of body weight gained (female, 39%; male 26%). These results are compared with other studies and their significance is discussed.

KEY WORDS   Carabidae, *Calosoma sayi*, *Spodoptera frugiperda*, food, starvation

The serious consideration of *Calosoma* (Coleoptera: Carabidae) species as potential biocontrol agents of defoliating lepidopteran larvae in the United States has continued for at least a century. Beginning with the classic compendium by Burgess and Collins (1917) of work done over the previous 20 yr, documentation is abundant concerning the role of *Calosoma* species as predators in forest ecosystems. Consideration has been minimal, however, of *Calosoma* species as biocontrol agents in row-cropping systems.

There are many characteristics of *Calosoma sayi* DeJean (Coleoptera: Carabidae) that would recommend it as a potential biocontrol agent in row crops. The species is abundant throughout the southeastern United States, occurring also as far west as Arizona and California and as far north as New York (Gidaspow 1959). Adults are well documented as predators of larval lepidopteran pests in several row crops of the southeastern United States (Price and Shepard 1978b, House and All 1981). This large (22–30-mm) species consumes not only a variety of larvae on the ground and on plant surfaces but also live adults of such pests as the spotted cucumber beetle (*Diabrotica undecimpunctata howardi* Barber), field crickets (*Gryllus* sp.), wireworms (*Melanotus* sp.), southern green stink bug [*Nezara viridula* (L.)], annual cicadas (*Tibicen* sp.), and a variety of dead arthropods (Young 1984). Consumption of adult stink bugs is particularly noteworthy, as many predators, including some carabid beetles, literally will not touch them (e.g., Kabacik-Wasylik 1971).

Several additional factors distinguish *C. sayi* as a predator in row crops. The species can reportedly produce two generations a year (Price and Shepard 1978a), and it can respond to increasing density of prey by increasing consumption (Price and Shepard 1978b). *C. sayi* also has been identified as having a potential role in the dissemination of two entomopathogens, a microsporidian protozoan, *Vairimorpha* sp., and a nuclear polyhedrosis virus. Both pathogens are lethal to lepidopteran larvae and are found in an infective form in the feces of *C. sayi* up to 15 d after the beetle has consumed diseased larvae (Young and Hamm 1985a). Adult beetles have demonstrated a life span of >100 d (Young 1985a), allowing for the possible consumption of considerable numbers of prey. The beetle also is large enough and has sufficiently strong mandibles to puncture and consume pupae of several lepidopterans, including the fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) (Young 1985b). Consumption of adult fall armyworm also is easily accomplished, because the wings are detached and discarded in the process (Young 1985a). Although *C. sayi* is primarily active on the soil surface and typically burrows into the soil as a daytime refuge, it will climb plants to attack prey, where it can capture resting or ovipositing adult moths, and larvae and pupae (O.P.Y., personal observations, field cage studies).

Although the amount of information involving *Calosoma sayi* has steadily increased over the last 20 yr, there are still considerable gaps in the knowledge

base. One important topic is the relationship of *C. sayi* to other natural enemies in field crops as they collectively exert pressure on crop pests. It is unlikely that *C. sayi* is the most important predator in any field crop ecosystem, but given its widespread distribution and abundance, as a member of the natural enemy community the species warrants further study. The effect of the enhancement, conservation, or reduction of *C. sayi* populations in field crops is unknown and should be experimentally determined. Many other aspects of the biology and ecology of *C. sayi* are unknown, such as knowledge of the weight gain and loss through the life span of the adult beetle, while feeding on various types of prey, as a means of assessing the lifetime potential of the beetle as a predator of agricultural pests. There is considerable information relating to the laboratory rearing of carabids to the adult stage (Weseloh 1998, Lundgren et al. 2005), but the maintaining of adult carabids in captivity, particularly *Calosoma* species, has been less well documented (Young 1985b, Young and Hamm 1986).

The present experiment was designed with ad libitum food to determine 1) the potential lifetime weight gain for an individual adult *C. sayi;* 2) how many feedings it would take to attain that weight; and then 3) how much weight if any would be lost over how long a period until death occurred, with food still available. An additional experimental goal was to determine any differences in the various stages of fall armyworm supplied as food that might be important to *C. sayi* in terms of weight gain and survival. All survival periods were compared with that of a "no food" group to ensure that *C. sayi* was receiving some benefit from fall armyworm consumption. A final calculation estimated the number of prey an adult *C. sayi* would consume over a lifetime. Because *C. sayi* may be a candidate for population augmentation as part of a suite of natural enemies, such information may be useful.

Materials and Methods

Adult *C. sayi* were obtained from a walk-in black-light trap surrounded by row crops located 6 km northwest of Tifton, Tift Co., GA, during 24–27 August 1981. Beetles were brought into the laboratory, examined for age and sex, with some subsequently maintained in separate soil-free containers at 10°C until the start of experiments. Those individuals that were dull colored and worn on edges of the clypeus and tibiae were considered to be adults of the previous year, and they were released. Individuals brightly colored with unworn edges of the clypeus and tibiae were considered to have recently eclosed, and they were retained (Young 2007a). On 28 August (day 1), each beetle was weighed on a Mettler A-30 balance and placed in a clear plastic container (17 by 12 by 6 cm) with a tight-fitting lid. A sheet of paper toweling was cut to cover the entire bottom and another sheet was crumpled and placed in a corner as a refuge. Water mist was applied to the toweling to provide humidity and drinking fluids. Containers were maintained at ambient laboratory conditions ($\approx$25°C and 75% RH) and exposed to the outside local photoperiod. Although *C. sayi* adults are normally active on the soil surface and routinely burrow into the soil, previous experiments had demonstrated that a comparison of longevity for *C. sayi* in containers with and without soil showed no significant differences (Young 1985a). These laboratory conditions have been successfully used with a variety of carabids, scarabs, and silphids (Young 1985c, 2005a, 2005b, 2006, 2007a, 2007b, 2007c; Young and Hamm 1985b).

Beetles were weighed at 7-d intervals, Fridays at noon, for 19 consecutive weeks. Individual beetles were initially immersed in water and washed to remove debris, air-dried 3–4 h in a clean container with a mesh lid, and then weighed. Previously occupied cages were emptied of papers and other debris, washed with weak disinfectant, air-dried, and clean papers added. Food was then placed in containers, on Mondays, Wednesdays, and Fridays. On each occasion, the condition of the beetle and its food was noted, water mist was added, and the appropriate food placed in the container. A somewhat different procedure was followed on Fridays, as noted.

The feeding protocol for each container was as follows: containers 1-8, 3 fall armyworm larvae (1); 9-16, 3 fall armyworm prepupae (2); 17-24, 4 fall armyworm pupae (3); 25-32, 8 fall armyworm adults (freshly killed by freezing and then thawed at room temperature) (4); and 33-40, no food, only water. Characteristics of the food items included the following: (1) 10 fall armyworm fifth/sixth instars: length, 25–30 mm; weight, 2.7683 g (=0.277 g per larva; (2) 10 fall armyworm prepupae: length, 20–25 mm; width, $\approx$5 mm; weight, 2.5603 g (=0.256 g per prepupa [prepupa=thick skin; shortened body, noncrawling, curled in silk chamber]); (3) 10 fall armyworm pupae: length, 15–18 mm; width, 4–5 mm; weight, 2.3651 g (=0.237 g per pupa); and (4) 10 fall armyworm adults: body length, 18–20 mm; weight without wings, 1.9068 g (=0.197 g per wingless adult).

The exception to the above-mentioned protocol was the treatment of four males and four females, in individual containers, obtained at the same time and place as others in the experiment. These eight beetles were not weighed at any time; their containers were cleaned and moistened once a week and the amount of food offered to each beetle was double the amount offered to other beetles—in this case, six live fall armyworm larvae (25–30 mm) three times per week. This procedure was designed as a control to assess both the impact of weekly weighing of beetles and the possibility that the amount of food offered in the main experiment was not adequate.

For statistical purposes, when a beetle was determined to be dead at one of the feeding occasions, it was considered to have died that day, after which it was washed, air-dried for 3–4 h, and weighed. The three beetles that were still alive at the end of the experiment (133 d) were considered to have died at that time. Statistical comparisons of the means of the various combinations of groups was accomplished by

Table 1. Mean values for *C. sayi* adults in each treatment (offered various stages of fall armyworm) and probability of significant differences

Observation	Larva	Prepupa	Pupa	Adult	No food
Start wt (g)	0.6357	0.6741	0.6706	0.6242	0.6591
Probability	a	a	a	a	a
Max wt (g)	0.8305	0.9420	0.8328	0.8239	0.6599
Prob.	a	a	a	a	b
% wt gain	30.98	40.26	25.64	32.55	0.10
Prob.	a	a	a	a	b
End wt (g)	0.6269	0.6386	0.6231	0.5976	0.5296
Prob.	a	a	a	a	a
Total days (start to end)	122.5	75.38	34.75	57.75	31.38
Prob.	a	b	d	c	d
% total wt gain or loss	−1.15	−3.53	−6.89	−3.76	−19.65
Prob.	a	a	a	a	b

Probability values read within rows; treatments with same letter are not significantly different; Newman–Keuls multiple comparison test (ANOVA); $n = 40$, $P < 0.05$ level.

use of the Student's *t*-test for comparisons of two means and a modification of the *t*-test (Newman–Keuls multiple comparison test) for comparing more than two means (Elliott 2004). On the unlikely possibility that the distributions of sample weights and survival periods were not normal, the nonparametric Mann–Whitney *U* test was performed, with results the same as with parametric tests. The level of significance used for all tests was <0.05.

Results

Activity Patterns and Feeding Behaviors. When food was first introduced to a container with an adult *C. sayi* occupant, the beetle would almost immediately emerge from hiding among the crumpled paper toweling and examine the food item. If the offering had been fall armyworm larvae, prepupae, or pupae, consumption of the first item could be completed within 20 min. All items usually would show some evidence of partial or complete consumption before the next offering several days later, although some prepupae and pupae frequently would appear untouched. When consumption had occurred, only the skin of the larva-prepupa-pupa would remain, as a deflated sack or empty shell with the contents removed. A trend was observed wherein initial offerings of prepupa and pupae were eagerly consumed, but later offerings were less so; no such trend occurred with offerings of larvae and adult fall armyworm. Comparing the sexes, females showed more interest than males in prepupae and pupae, the males sometimes seemingly avoiding the items. No differences were observed when other foods were offered. When eight adult fall armyworm were offered to individual beetles, at no time were all eight consumed before the next feeding. Considering all situations where live food items were offered, there was no instance when the beetle seemed to be attacking more prey than it would eventually consume. Thus, rather than attempting to initially kill every prey item in the container, the beetle would first attack and consume a prey item, then either return to a refuge or attack and consume an additional prey, continuing the sequence until either the beetle was satiated, all food was consumed, or a fresh set of food items was added.

Those beetles deprived of food showed the same change in activity pattern as demonstrated by Grum (1966) with five carabid species. During starvation, beetles first increased activity within the normal nocturnal period, then shifted activity to the diurnal period while reducing overall activity. All beetles exhibited the same behaviors when death was imminent. Within a few days of death, the beetle would become sluggish, eventually stopping ambulatory movement, and finally expiring after various twitching movements. When food was present, those last few days also involved a decrease in activity associated with food, in most cases evidenced by apparently ignoring food items. The overall sequence of behaviors showed no differences between the beetles dying from apparent starvation (deprived of food) and those dying from apparent senescence (food ad libitum). Subsequent examination of dead beetles showed no evidence of mites, fungi, parasites, or other possible lethal agents.

Specific Trial Results. Considering the four *C. sayi* groups offered food and the one group denied food (Table 1; $n = 40$; Newman–Keuls multiple comparison test), there were no significant differences in the starting weights of the five groups, or the end (terminal) weights. As expected, the group deprived of food was significantly different from all other groups in the maximum weight obtained, the percent weight gained, and the total percentage of weight loss from start to termination. The total number of days from start to end for each group showed significant differences between all groups except between the no food and the pupa groups. Beetles offered three fall armyworm larvae per feeding lived significantly longer (122 d) than any other fed group, whereas the no food group and the group offered pupae were the shortest lived (31 and 34 d, respectively).

Comparing *C. sayi* males with females, and including the group deprived of food (Table 2; $n = 40$; Students *t*-test), the only significant difference was in the starting weight, higher for males. Comparing males with females, but excluding the group deprived of food (Table 3; $n = 32$; Students *t*-test), the mean starting weight for the male group was significantly larger than for the female group, but the percent weight gain for the female group was significantly larger. There were

Table 2. Mean values for *C. sayi* adults of each sex offered various stages of fall armyworm; includes all five feeding groups

Observation	20 males	20 females	Probability[a]
Start wt (g)	0.6825	0.6231	0.022*
Start to max (d)	24.50	26.44	0.751
% wt gain (start to max)	22.98	34.58	0.078
Max wt (g)	0.8224	0.8132	0.843
Max to end (d)	43.2	40.1	0.668
% wt loss (max to end)	24.57	26.60	0.463
End wt (g)	0.6150	0.5914	0.420
Start to end (d)	65.15	63.55	0.890
% wt gain or loss (total period)	−9.53	−4.70	0.160

[a] Student's *t*-test for probability of significant differences (*) at 0.05 level (*n* = 40).

Table 3. Mean values for *C. sayi* adults of each sex offered various stages of fall armyworm (excludes the no food feeding group)

Observation	16 males	16 females	Probability[a]
Start wt (g)	0.6826	0.6198	0.038*
Start to max (d)	26.69	28.88	0.699
% wt gain (start to max)	25.83	38.88	0.012*
Max wt (g)	0.8572	0.8573	0.999
Max to end (d)	45.69	43.94	0.838
% wt loss (max to end)	25.16	28.92	0.231
End wt (g)	0.6359	0.6073	0.364
Start to end (d)	72.38	72.81	0.973
% wt gain or loss (total period)	−6.39	−1.35	0.160

[a] Student's *t*-test for probability of significant differences (*) at 0.05 level (*n* = 32).

no significant differences between the sexes in the other measured parameters.

Differential Response between Sexes. The starting weights of the beetles as a group (*n* = 40) were significantly different between the sexes (males heavier), but no subset (*n* = 8) representing any of the five feeding groups showed significant differences (Table 4). Looking at each feeding regime separately while comparing the mean percentage of weight gain of each sex, from start to maximum (Table 4), there were significant differences in the fall armyworm pre-pupa and pupa feeding regimes and a substantial difference (*P* < 0.10) between the sexes when all five regimes were combined. Comparing the mean percentage of weight gain or loss from start to end (Table 4), none of the feeding regimes showed significant differences between the sexes, although the response of males to fall armyworm pupa (−15.6%) was substantially different (*P* < 0.10) than females (+1.8%). Looking at each feeding regime separately while comparing the mean period of survival of each sex (Table 4), there were no significant differences within any of the feeding regimes, which was also true when the five feeding regimes were combined.

Response to Different Amounts of Food. The comparison of *C. sayi* survival periods for individual beetles offered three or six fall armyworm larvae three times a week (Table 5) demonstrated a significant difference (Student's *t*-test, *n* = 16, *P* < 0.01), with those beetles offered the larger amount of food surviving a shorter period of time (108.5 d) than those beetles offered less food (122.5 d).

Discussion

Weight Gain and Loss. The rate of weight gain is not easily comparable with that demonstrated in other experiments. The maximum weight gain values in Table 1 (25–40%) required ≈25 d from the start of feeding (Table 2). Most investigators, however, have documented the weight gain of beetles after only one feeding after starvation. As an example, a study in Canada involving a *Calosoma* similar in size to *C. sayi* (*Calosoma calidum* F.; occurs in Georgia) demonstrated that after 1 h of feeding the body weight of individual beetles had increased ≈26%, but after 47

additional hours without feeding the total weight gain had been reduced to 10%; 48 additional hours without feeding reduced the weight gain to 3% (Cheeseman and Gillott 1987). In that study, 59% of the weight gained at feeding was lost within 2 d, and 91% lost in 4 d. This and similar research was associated with the role of *C. calidum* and *C. frigidum* Kirby as natural predators and potential biocontrol agents for the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantridae) (Jeffords and Case 1987, Cameron and Reeves 1990). In another study involving *Calosoma affine* Chaudoir from California, the mean consumption rate during the first 12 h represented 60% of the initial body weight of the beetle (Wallin 1991). Carabids such as *Calosoma* spp. that feed exclusively on other insects typically consume <1 times body weight daily (van Dinther 1966, Wallin 1991), whereas carabids that are polyphagous and consume a large percentage of plant material may consume >2 times body weight daily (Thiele 1977). Although fecal material associated with a meal can occur in *C. sayi* feces in <12 h (Young and Hamm 1986), complete digestion of a meal probably requires 3–5 d (Cheeseman and Gillott 1987, Chaabane et al. 1994). In the experiment described herein, beetle weights were not obtained immediately after feeding, but 2 d after the previous feeding and after a total of three feedings. Even with these differences, an analysis of the weight gain in the first week of the experiment, after three feeding and 48 h after the last feeding, obtained values of 14–25% for the 32 beetles offered food (Table 6).

Male carabid beetles may be more vulnerable than females to food-related activity. Szyszko et al. (2004) demonstrated that males and females of a *Carabus* (Carabidae) species were equally active when both were hungry, but when both were satiated, the males were much more active. The relative amounts of food consumed by each sex before satiation also may vary. Working with a *Carabus* species, von Lengerken (1921) demonstrated that the males consumed much more food than females (no indication of survival period). Conversely, Chaabane et al. (1994) showed that females of an *Abax* (Carabidae) species ate more and gained more weight than males. The experiment described herein indicates that at the very least, fe-

Table 4. Differential response between sexes of adult *C. sayi*

Treatment	Male	Female	Probability[a]	n
	Mean starting wt on five feeding regimes			
Larva	0.6525	0.6190	0.569	8
Prepupa	0.7355	0.6127	0.188	8
Pupa	0.7138	0.6275	0.129	8
Adult	0.6285	0.6200	0.845	8
No food	0.6823	0.6360	0.430	8
Total	0.6825	0.6231	0.022*	40
	Mean % wt gain, from start to max, on five feeding regimes			
Larva	31.63	30.33	0.869	8
Prepupa	31.98	48.55	0.007*	8
Pupa	2.63	48.65	<0.001*	8
Adult	37.10	28.00	0.105	8
No food	0.1	0.1	1.0	8
Total	22.98	34.58	0.078	40
	Mean % wt gain or loss, for entire period, on five feeding regimes			
Larva	2.10	−4.40	0.178	8
Prepupa	−4.10	−2.95	0.850	8
Pupa	−15.63	1.85	0.079	8
Adult	−7.95	0.43	0.363	8
No food	−22.08	−17.23	0.170	8
Total	−9.53	−4.70	0.160	40
	Mean period of survival (d) on five feeding regimes			
Larva	117.25	127.75	0.261	8
Prepupa	82.25	68.5	0.202	8
Pupa	28.75	40.75	0.164	8
Adult	61.25	54.25	0.591	8
No food	36.25	26.5	0.136	8
Total	65.15	63.55	0.890	40

[a] Student's *t*-test for probability of significant differences (*) at 0.05 level.

males of *C. sayi* gain significantly more weight that males (Table 3) and hence are probably eating more, yet when consuming food live just as long as males (Table 3).

Survival Period. Restricting the diet of *C. sayi* to only one life stage of the fall armyworm did not have a significant impact on the maximum weight gained, the percentage of weight gained, the terminal weight, or the percentage of weight lost (Table 1). That result does not indicate, however, that there were no differences in the effect of the restrictive diets on the well being of the beetles. The significant differences in the survival period of beetles on the various diets

Table 5. Comparison of survival periods (d) for individual *C. sayi* adults offered either 3 or 6 FAW larvae, three times per week, until death or end of trial at 133 d

Gender	Three fall armyworm larvae	Six fall armyworm larvae
Male	101	82
Male	112	103
Male	129	105
Male	133[a]	122
Female	124	101
Female	129	112
Female	133[a]	115
Female	133[a]	126
Mean	124.25	108.25
	$P < 0.01$**	

[a] Beetles alive at end of trial.
** Student's *t*-test.

indicate real nutritive differences in the diets (Table 1). Although *C. sayi* adults are well documented predators on pupae of various lepidopterans (Price and Shepard 1978b, Brown and Goyer 1984), exclusive consumption of fall armyworm pupae, or prepupae, or adults, significantly reduces the life span of the adult beetles as compared with consumption of fall armyworm larvae (Table 1). Thus, there seem to be negative components of a polytypic diet that would include several life stages of a lepidopteran, at least for *C. sayi* consuming fall armyworm. Given that an exclusive diet of fall armyworm pupae is probably unusual for *C. sayi* under field conditions, some other members of the genus seem to be much better at accommodating unusual diets. For example, McCullough (1966) was able to maintain on a diet of bananas a pair of adult *Calosoma scrutator* (F.) over a period of 206 d, during which the beetles actually gained weight.

The lack of significant differences in the survival periods for those beetles consuming only fall army-

Table 6. Mean weight and percentage values for *C. sayi* adults offered various stages of fall armyworm

Life stage	Starting wt	wt after 1 wk	% wt gain
Larva	0.6357	0.7253	14.1
Prepupa	0.6741	0.8453	25.4
Pupa	0.6706	0.8108	20.9
Adult	0.6242	0.7575	21.4
Mean	0.6510	0.7847	20.5

Table 7.　Values of parameters associated with the maximum weight gained by adult *C. sayi* on four feeding regimes of fall armyworm

Fall armyworm stage (no. items per feeding)	Mean wt gained (start to max, g)	Mean no. feeding	Mean no. food items	Mean total wt of food items (g)	Ratio of mean wt consumed to mean wt gained
Larva (3)	0.1948	20.25	60.75	16.77	86.4
Prepupa (3)	0.2679	9.38	28.14	7.20	26.9
Pupa (4)	0.1622	4.88	19.52	4.63	28.5
Adult (6[a])	0.1987	13.13	78.78	15.52	78.1

[a] Although eight fall armyworm adults were offered at each feeding, at no time did more than six show subsequent evidence of feeding by the beetles.

worm pupae and those deprived of food (31 versus 35 d, Table 1) was not anticipated. Those similar survival periods were attributable to sexual differences in the acceptability of pupae. The four males gained only 2.6% body weight consuming pupae, whereas the four females gained 48.6% body weight, a highly significant difference (Table 4). Given that large weight gain by females, it was surprising that the female total weight gain for the entire period was only 1.8% (Table 4), indicating that they also lost a lot of weight during the period and only survived somewhat longer than males on the pupal diet (Table 4). It is possible that females, before producing eggs and facing the high protein needs associated with that production, could selectively chose prey such as lepidopteran pupae that are a more concentrated source of nutrients than the associated larvae. Under field conditions the females could eventually switch to larval or adult forms, something that the experiment did not allow, thus forcing them to continue feeding on a prey item that possessed some deleterious factors when consumed in excess. To reinforce the conclusion that prepupae and pupae are a more nutritious food source for *C. sayi*, an alternate analysis is to relate the maximum amount of weight gained in the four feeding regimes to the total weight of the presumptive prey consumed in that period from the start of the experiment to the achieving of maximum weight (Table 7). *C. sayi* adults, even when the sexes are combined, consumed one third less weight of fall armyworm prepupae or pupae to reach their point of maximum weight gain, compared with the consumption of fall armyworm larvae or adults.

Significant differences in survival period between the sexes is the typical result in beetle feeding trials, although such was not the case in this experiment (Table 4). Labitte (1916) maintained eight beetle species in captivity, with females of six species living longest. Rockstein and Miguel (1974) evaluated survival periods of 19 beetle species in five families, and they found that females lived longer in 16 species. Kabacik-Wasylik and Stejgwillo-Laudanska (1971) showed with two carabid species that females lived significantly longer without food than males (35.5 versus 23.5 d).

The relative amount of body weight lost by *C. sayi* during starvation, 19.65% (Table 1), is somewhat less than published values for other carabid species. Laboratory studies with a *Carabus* sp. (similar size to *C. sayi*) showed a 25% weight reduction after seven days of starvation (Grum 1966). Maintaining six carabid species in captivity without food, van Dinther (1964)

demonstrated survival periods ranging from 12 to 116 d, with the mean body weight loss at death ranging from 25 to 47% and 12 to 25% of that weight loss occurring in the first 2 d. In a study involving two carabid species, Kabacik-Wasylik and Stejgwillo-Laudanska (1971) showed that after 28 d without food, males lost 57% and females lost 67% of body weight.

One factor working against the survival of beetles without food is the associated level of activity. Working with five predaceous carabid species, Grum (1966) showed that starved beetles initially increased activity for a considerable period, eventually decreasing activity to a low steady state before death. Working with 12 predaceous carabid species (including a *Calosoma*), Wheater (1991) demonstrated that starved insects were more active (traveled further) than well-fed insects (sex not indicated); such increased activity surely decreased stored energy reserves faster than more normal activity levels and apparently hastened their eventual death.

An initial assumption of the experiment was that *C. sayi* adults offered food until death would not die of starvation, but would slow down, enter senescence, and then die of "natural causes." It was therefore surprising that beetles in all four regimes containing food died weighing less than when the experiment started, even though all four groups had gained from 25 to 40% of body weight during the experiment. It has not previously been documented that natural causes of death in carabids can functionally involve starvation in the presence of easily obtainable food. The more typical sequence is demonstrated by adult *Oryctes rhinoceros* L. (Coleoptera: Scarabaeidae), which when food is ad libitum, at death weighs 35–44% more than at adult emergence (Vander Meer 1987).

Confounding Factors. One factor having a potential major impact on the results of this experiment is the sufficiency of the amount of food offered. Previous research with *C. sayi* had provided some information, but the strategy chosen in this experiment to determine the sufficiency of food was to ensure that more food was provided than was consumed. For example, two fall armyworm larvae (30 mm) offered to one adult *C. sayi* two to three times a week had been sufficient in previous research (Young 1985a). Monitoring the level of consumption in this experiment indicated that offering three fall armyworm larvae three times a week left some larvae undamaged, indicating a possible satiation. To address the issue in another way, an experimental control was initiated (Table 5) comparing the survival period of beetles

offered either three or six fall armyworm larvae (30 mm) three times a week. Additional food (six larvae) did not extend the life span of the beetles longer than those receiving less food (three larvae), indicating that the three-larvae level of food availability in this experiment was adequate for *C. sayi* under these laboratory conditions. What was not anticipated was the significantly shorter survival period for those offered the most food. It would seem that the likely increased consumption (six versus three fall armyworm larvae) shortens life span (124 versus 108 d), suggesting that the potential amount of prey consumed over an adult life span may be relatively constant, with the length of that life dependent on the rate of consumption. Such a relationship has been demonstrated in other arthropods. In laboratory experiments with the spider *Frontinella pyramitela* (Walck.) (Araneae: Linyphiidae), Austad (1989) demonstrated the effect on life span of varying the amount of daily food. Three sets of spiders fed different amounts of food until death resulted in the most amount of food yielding the shortest life span— 42 d, an intermediate amount of food— 64 d, and the least amount of food—81 d.

The choice of the various fall armyworm life stages as exclusive food items for different sets of beetles may have a priori negatively affected survival periods. It is unlikely that an individual *C. sayi* adult under normal field conditions would be restricted for its entire life to one life stage of one species of prey. Although this experiment demonstrated a negative effect of exclusive prepupae, pupae, or adult consumption compared with larval consumption (Table 1), all survival values were probably depressed due to the monotypic nature of the diets. Working with two species of cursorial ground spiders, Uetz et al. (1992) indicated that spiders consuming a monotypic, as opposed to a polytypic, diet had a lower survivorship, later sexual maturity, and a smaller body size at maturity, demonstrating fitness-related consequences of dietary breadth. Other factors in the present experiment, however, may have extended the survival period of the beetles. The maintaining of individual *C. sayi* adults in separate containers, with the resultant prevention of reproductive interactions between the sexes, may have extended their life span. Such a phenomenon has been demonstrated with members of the carabid genus *Carabus* (Krumbiegel 1930, cited in Rockstein and Miguel 1974).

Other conditions of the experiment may have had positive or negative effects on beetle survival. *C. sayi* is diurnally phototaxic negative as an adult (Price and Shepard 1978b); thus individuals in this experiment were much more active during the day than if they had been in containers with soil into which they could have burrowed and remained until nighttime. This increased activity in soil-less containers, however, though potentially having a negative impact on energy reserves, has been demonstrated to have no effect on long-term *C. sayi* adult survival when compared with survival in containers with soil (Young 1985a). The procedures employed in this experiment to obtain the weekly weights of individual beetles were initially

thought to have potentially negative impacts on the length of the survival period. The weekly washing, drying, and weighing of each beetle, when eliminated for a set of eight beetles offered three fall armyworm larvae three times a week (Table 5), however, did not substantially alter their life span (mean = 124.25 d) compared with the main experimental group (Table 4) offered the same food at the same frequency (mean = 122.5 d). The choice of fall armyworm larvae of a certain size as a food item, although potentially excluding acceptable sizes, was based on previous experiments. *C. sayi* adults have a preferred size range for fall armyworm larvae consumption, ignoring anything smaller than ≈10 mm in length, and avoiding larvae considerably larger than 30 mm (Young 1984). Some lepidopteran larvae can become too large or aggressive for *C. sayi*, such as 80-mm tobacco hornworm [*Manduca sexta* (L.)] larvae, requiring at least two *C. sayi* individuals to subdue (Young 1984).

C. sayi as a Biocontrol Agent. What does this experiment say about the potential of *C. sayi* as a biocontrol agent in southeastern U.S. row crops? An effective biocontrol agent against crop pest(s) would include as one of its characteristics the ability to have a major impact on the most injurious life stage of the pest(s). Although *C. sayi* attacks the stage (larva) of the fall armyworm that does the damage to crops, attacking the adult female before eggs are deposited would have the most impact on the subsequent pest populations. Given that *C. sayi* may only infrequently capture an adult female fall armyworm, and perhaps only slightly more frequently consume a fall armyworm female pupa, its impact on fall armyworm populations may be relatively small.

Some investigators have noted large larval consumption rates for adult *C. sayi* over a short period, and they have concluded that the predator has considerable biocontrol potential. For example, Brown and Goyer (1984) indicate that *C. sayi* is capable of consuming 16 sixth instars of *Pseudoplusia includens* (Walker) (Lepidoptera: Noctuidae) larvae in 24 h, although size of larvae or subsequent feeding history and longevity are not noted. The experiment described herein suggests that high initial consumption rates by *C. sayi* adults, if continued, could lead to a shortened life, reducing their potential impact on a prey population. Burgess and Collins (1917) conducted feeding experiments with many adult *Calosoma* species, including the six species occurring in Georgia. Offering ad libitum sixth stage larvae of *Malacosoma americanum* (F.) (Lepidoptera: Lasiocampidae) and/or *Porthetria dispar* (now *Lymantria dispar*) (Lepidoptera: Lymantriidae) during the period from early summer to fall hibernation of the adult Georgia *Calosoma* species, they obtained consumption values of 75–315 larvae per pair of beetles. For the experiment described herein, assuming every fall armyworm larvae that was offered (nine per week) was consumed, and that the average consumption period was 122 d before death (Table 4), one *C. sayi* individual may have consumed as many as 156 fifth-sixth instars of fall armyworm. This probable overestimate

is compatible with the probable underestimates of Burgess and Collins (1917). Whether this consumption value demonstrates *C. sayi* to be a superior predator on lepidopteran larvae is undetermined.

This experiment provides no evidence that *C. sayi* adults live more than one season, which does reduce their potential as consumers of crop pests. Other *Calosoma* adults, such as *C. sycophanta*, can live up to 4 yr and have considerable potential as biocontrol agents (Burgess and Collins 1917, Weseloh 1985). One measure of the effectiveness of a biocontrol predator is how many prey pests it kills; whether it consumes them all is not necessarily relevant. This experiment provides no evidence that *C. sayi* kills more prey than it can consume, which also reduces its potential effectiveness as a biocontrol agent.

C. sayi forages primarily on the ground, although it can occasionally venture into crop canopies to obtain prey. *Calosoma* species that are equally adept on and above ground have been shown to be important biocontrol agents. European and Japanese studies with *Calosoma inquisitor* L. and *Calosoma maximowiczi* Morawitz have documented their importance as natural regulators of defoliating caterpillar populations both in trees and on the ground (Cook 1936, Kamata and Igarashi 1995). Research in the United States has examined similar multilevel species such as *C. callidum* and *C. frigidum* (Cheeseman and Gillott 1987, Snider and Snider 1997). Species such as *Calosoma sycophanta* (L.) that are arboreal specialists on specific prey have been used as effective biocontrol agents (Burgess 1911, Schaefer et al. 1999). There are no primarily ground-active *Calosoma* species that are currently being used, or even being seriously considered, as biocontrol agents against row crop pests. The available evidence thus indicates that *C. sayi*, although a well-recognized member of the predatory arthropod complex in row crops and certainly worthy of conservation, is not a good candidate for specific development as a biocontrol agent for crop pests.

Acknowledgments

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